XXVII. *Observations on the Development of the Theca, and on the Sexes of Mosses.* *By* William Valentine, *Esq., F.L.S.*

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THERE is, perhaps, no part of the physiology of plants involved in deeper mystery, or about which there is a greater diversity of opinion, than the sexuality of Mosses. Of all the theories which have hitherto been presented to the notice of physiologists, that of the celebrated Hedwig has obtained by far the greater number of followers. He described two kinds of organs constituted, in his opinion, for the purpose of reproducing the species,—the male, or spermatocystidium, the female, or pistillum: the former being a pedunculated oblong sac, containing a fluid mixed with a granular pulp, which is discharged with some force from the sac on the application of water; the latter, after the admission of the *semen masculinum* by means of the stigma and tubular style, enlarging to form the fruit. All that has been hitherto known about this body is, to use the words of Professor Hooker (*Muscologia Britannica*, Introduction, ed. ii. p. 11.), that "the base of one of the pistils gradually swells more and more, and after a certain period the upper part of the style and stigma withers, but still remains. The germen is now seen, covered by a thin membrane, which, as the fructification advances, separates transversely at the bottom, and rising up with the more advanced germen, takes the name of calyptra, or veil. It is carried up by means of a pedicel, or fruitstalk, which now develops itself and reaches to a different height in different species, in some being five or six inches in length. When it has attained its utmost development, the mature germen becomes the perfect fruit, and is called the capsule." We find in this passage the opinion that the capsule, or theca as it is now more properly named, is formed in the first instance, and carried upwards by the subsequent development of the fruitstalk or seta. There are generally several of these pistilla together; they are

often mixed with jointed pellucid filaments, "*fila succulenta*" of Hedwig, and in some cases accompanied by the supposed stamens, which in others grow on a different part of the same plant (monœcious), or on a distinct plant (dicœcious). The object of this paper is chiefly to explain the anatomy of these pistilla, their structure being such as to throw considerable light upon the sexual theory. I was first led to examine this subject by discovering the highly curious fact, that the setæ of Mosses and the Jungermannias terminate downwards in a cone, which is inserted within a corresponding cavity of the branch, to which it has but a very slender attachment; or, in other words, that the seta has very little if any organic connexion with the plant. This structure appeared to be so anomalous, that I determined on the first opportunity to investigate the cause. The following observations are the result*.

In the very young state the pistillum contains a single unconnected oval transparent body or cell, which is situated about one third from the base. The pistillum, as yet, has not begun to enlarge, but is of one uniform diameter. The cell is present before the apex of the pistillum has burst open to form the stigma; and consequently before there is any communication, by means of the tubular style, with the external air. This canal, however, is formed before the bursting open of the apex, and leads directly down to the cell, which appears to be situated in its lower extremity. The cell may be distinguished through the walls of the pistillum with the assistance of a good Wollaston doublet, and I have succeeded in dissecting it out uninjured. It was of a firm texture, a quality depending probably on the thickness of the membrane; it was also beautifully pellucid, and contained a quantity of moving particles. Upon pressing it with a piece of talc it burst, and the moving particles escaped. Its diameter was between the one thousandth and the one five-thousandth of an inch. Generally one or two only of the pistilla in the same bud arrive at perfection, and the abortive ones are destitute of this cell; whilst, on the contrary, in *Bryum ligulatum* nearly all the pistilla, sometimes amounting to between twenty and thirty, become fruit, and in every one of them may the cell be detected. *Bryum roseum* very rarely

* Since this was written, I have been favoured by Mr. Brown with a sight of Hedwig's *Fundamentum Historiæ*, &c., in which this structure is figured. It is surprising that this remarkable peculiarity should not be anywhere noticed, either by Hooker, Greville, or, indeed, any of the British muscologists.

indeed produces fruit in this country; but in the winter it not uncommonly possesses healthy-looking pistilla. I have, however, never been able to detect the cell in any of them. The manner of the development of this body is exceedingly simple. Soon after the opening of the upper extremity of the style another cell is formed on the upper surface of the first. The two adhere firmly to each other, and may be dissected out together. Presently another cell is formed, either on the upper surface of the second, or on its side; then appears another, and so on gradually increasing in number. When about ten cells are developed the dissection becomes comparatively easy, and the oblong mass may be exposed, with the original cell still remaining at the base. In this stage it has become rather flattened on the upper surface from the pressure of the newly-formed cells.

Whilst this process is going on, the base of the pistillum itself increases in size, not by distention, as is universally supposed, but by the addition of fresh matter. At the same time the style becomes of a red or brown colour, of a rigid texture, and never increases in size after the opening of its canal. In *Funaria hygrometrica* the pistillum elongates considerably before the base has increased in diameter, to allow of the rapid growth of the oblong or fusiform mass within, which now occupies its whole length from the apex immediately beneath the hardened style to the very base, and even beyond, having pushed its conical extremity deeper into the tissue, until at last it has actually penetrated the branch itself. After the pistillum has attained a considerable length, its base increases in diameter without a corresponding increase of the central body, so that a space is left between the two. Very shortly the pistillum separates transversely below the dilated portion, and is supported on the apex of what may now be called the seta, by the more rapid elongation of which the separation has been caused. At this period may be observed a sheath of elastic gummy secretion, embracing the base of the seta, immediately opposite the point of separation between the upper part of the pistillum (now called the calyptra) and the base, which receives the name of vaginula. This sheath of mucous gradually becomes solid and cellular; and, by its connexion with the vaginula and its firm embrace of the seta, serves to secure the latter in its cavity.

The extremity of the seta is not invariably conical. The exceptions, how-

ever, appear to be few, as I have only detected three out of the very great number of species I have examined. In *Sphagnum* it is shaped somewhat like a button, having a very narrow neck, which is firmly embraced by the vaginula. This narrow neck is the only seta which exists in this genus, so that the theca is placed immediately on the vaginula. Muscologists, from not understanding the anatomy of this part of mosses, have denied the presence of a vaginula in the genus *Sphagnum*. Dr. Greville and Mr. Arnott, in their excellent memoir published in the Wernerian Transactions, have indeed maintained the existence of the vaginula; but they have described as such what ought not to be so considered. In this genus the calyptra, instead of dividing at the point where the sheath of mucus is secreted around the seta, is torn irregularly across the middle by the enlargement of the theca; and the scarious portion, which remains loose about the base of the theca, these observers have mistaken for the vaginula. The true vaginula, which is dilated and lentiform, to accommodate itself to the button-like termination of the seta, they call the receptacle, from not being aware of the internal structure. Another variety in the figure of the termination is in *Schistostega pennata*, where it is obovate, and the vaginula very much resembles in appearance the theca. But the most curious exception is in *Dicranum flexuosum*, in which the form is conical, but instead of being straight, is bent completely on itself. This structure can only take place by the second cell being developed on the under surface of the first instead of on the upper, as happens in all other cases. The succeeding cell is placed transversely, and the rest assume the normal direction.

To return to the progress of the development. A period of a month or more follows the separation of the calyptra without any further change taking place than the gradual elongation of the seta. In some instances, as *Encalypta vulgaris*, *Tortula ruralis*, and many more, three or four months are occupied by this process. The seta elongates by the addition of new matter *at the apex*, where it is always of a more delicate texture than nearer the base. The cells are also more crowded, less distinct in their outline, and have as yet no cavity. The further you examine from the apex, the more decidedly does the tissue become cellular, until it has arrived at maturity, when the cells are considerably elongated. After attaining a length, varying in each species

according to circumstances, the seta gradually enlarges in diameter at the apex, and imperceptibly assumes the form of the theca. A section of the dilated apex, if made at an early period, will exhibit a central portion and a cortical layer, only differing from the structure of the seta itself by being more distinctly defined. As the theca advances towards maturity, the cortical layer gradually recedes from the central axis, but is still connected with it by little transverse fibres, or rather strings of cells, which pass from one surface to the other without apparent arrangement. The axis, or columella as it is now termed, is supported on a pedicel which is continuous with the central tissue of the seta; whilst the outer layer, or true theca, is an expansion of the external layer of the seta. Surrounding the theca, near the apex, is a faint line, which indicates the situation of a transverse dehiscence to take place at the perfect maturity of the theca. The portion above this line varies considerably in figure, and is called the lid, or operculum. The ring or orifice of the theca, formed by the fall of the operculum, is called the mouth or stoma. It is necessary to name these parts in this stage of the development, to explain clearly the succeeding steps of the process.

The distance of the columella from the theca varies in each species; in many being but trifling, whilst in some it is considerable, as in *Gymnostomum pyriforme*. But in none is it so remarkable, so far as I have examined, as in *Bartramia pomiformis*. In this plant the columella is borne on a pedicel even longer than itself, and only occupies a small space in the upper and middle part of the theca. A section of the columella, in this stage, exhibits a trace of division into an external layer and a central axis. This external layer is gradually pushed outwards (until it comes in contact with the theca) by the formation of the sporules, between it and the axis to which the name columella is with greater strictness applied. The layer itself has received the name of internal or lining membrane of the theca; but as I have ascertained the presence of a distinct and very important lining membrane to that part, it will be more convenient to assign the name of columellar membrane to this, as to the columella it assuredly most naturally belongs. The cavity in which the sporules are developed is closed on all sides, being bounded at the centre by the columella, and at the circumference by the columellar membrane, which passes outward from the base of the columella to the theca, on

the inner surface of which it is reflected upwards to the stoma. The membrane is attached to the stoma all round, frequently by a distinct process; and after forming this attachment, it passes horizontally inwards, and becomes again continuous with the columella at its apex. Until about the period of maturity, or a little earlier, the columella is continuous from the base of the theca up to the arch of the operculum, when a transverse line (indicating a tendency to separation) appears above the point of its connexion with the columellar membrane. Most commonly this separation does actually take place, and the upper portion falls with the operculum. This portion was first described and named, very appropriately, by Greville and Arnott, the opercular membrane. I have observed in one instance, the *Hymenostomum* of Brown, the columella to separate below as well as above the point of connexion with the columellar membrane. The opercular membrane, when mature, either remains attached to the columella, falls with the operculum, or (in the genus *Polytrichum*) shrivels from below upwards, and remains attached to the apices of the teeth of the peristome in the form of a horizontal membrane or tympanum.

In an early stage the inner layer of the operculum separates in the form of a distinct membrane, which, ultimately dividing longitudinally into a definite number of processes or teeth, forms the peristome. In some rare instances this membrane never breaks up into teeth, as in *Diphyscium*; whilst in one instance, *Buxbaumia*, it is double; the external splitting into ciliæ, and the internal remaining entire. At the same time that this membrane is formed from the operculum, the opercular membrane forms another, immediately within the first, by a separation of its exterior series of cells. This also, more or less, divides longitudinally into a determinate number of teeth, thus forming the inner peristome. The number of teeth forming each of these peristomes has been ascertained by muscologists to be either four, or a multiple of that number*. The outer peristome is universally considered to arise from the theca itself; whilst the inner is believed to arise from the internal membrane,

* Mr. Brown appears to have been the first to point out the mode of ascertaining the true number of the teeth. This great botanist reduces the number of the outer series in most instances to thirty-two. Vide Linnean Transactions, vol. xii. p. 577., where may be found some excellent observations on this subject.

or columellar membrane of this paper. The necessity of substituting this name will presently appear. To say that the outer peristome *arises* from the theca would give an incorrect idea both of its origin and connexion. It is *continuous* at the base, with a delicate lining membrane, which is very intimately attached to the theca. The existence of this lining membrane, which has hitherto escaped the notice of observers, may be proved by taking a portion of the theca from which the columellar membrane has been detached, and carefully separating the peristome from above downwards, when the lining membrane will remain attached to the base. A very thin longitudinal section will also show the division of the theca itself into an external and internal layer. The former, when mature, is of a dense coriaceous or even horny texture; whilst the latter is of a loose spongy cellular tissue. The most favourable examples to prove this fact by dissection are found in the genus *Tortula*; but the Hypnums, a genus very remote from *Tortula*, are by no means unfavourable. The term lining or internal membrane ought properly to be applied to this newly described layer; but, to prevent confusion, it appears desirable to abandon the use of this name altogether, and to supply its place with the term columellar membrane, designating the proper lining of the theca the thecal membrane. The inner peristome is continuous with the columellar membrane, at the point where this last is attached to the inside of the stoma. These peristomes are not always formed. Some genera are altogether destitute of them, whilst others have only one, which, as far as my observations have gone, is always the external. Dr. Hooker, in the Linnean Transactions, vol. ix. p. 310, describes the single peristome of *Pterogonium declinatum*; and Bridel, the membranous ring of *Hymenostomum*, as arising from the columellar membrane. With regard to the first plant I cannot give any positive evidence; but it seems probable that Dr. Hooker was mistaken, from not being aware of the presence of a thecal membrane. This probability is strengthened by the facts that the peristome of *Pterogonium intricatum*, another species of the same genus, arises from the thecal membrane; and *Pterogonium gracile* has actually a double peristome. As to the origin of the peristome in *Hymenostomum* I can speak with greater certainty, as I have frequently dissected away the columellar membrane entire; and the peristome was in every case left attached to the thecal membrane. This latter peristome,

although it follows the law above stated, is very anomalous in other respects. It is a horizontal membranous ring, formed between the opercular membrane and the horizontal portion of the columellar membrane. This situation precludes the possibility of its having been formed by the separation of the internal layer of the operculum.

It is now necessary to describe the development of the sporules. The period at which this process commences is rather uncertain; most probably it begins at the time of the separation of the columellar membrane from the columella. Dr. Hooker in the *Flora Londinensis,* vol. iv. fasciculus i., under "*Diphyscium foliosum,*" has this passage: "It would be curious to ascertain, were it possible, what becomes of the substance forming the cellules in the early state; for the ripe seeds are quite free and unconnected, yet not separated by any membranous substance such as the walls of the cellules appear to have been formed of. On the contrary, they occupy a cavity around the columella, which appears evidently to be nothing more than the remains of the cellular and pulpy substances in which the seeds have not been perfected, and which, as we may consequently expect, when dry, shrinks up into an angular axis or columella, as it is called by Hedwig and other muscologists." Mr. Brown, in the Linnean Transactions, vol. x. p. 315, says, in speaking of what he names the placentation of the seeds: "That in some cases the seeds may be formed in a much greater portion of the columella than in others: and it is even not improbable that in certain cases its whole substance may be converted into seeds: or, to speak more accurately, that it may produce seeds even to the centre, and that the cells in which they were probably formed may be reabsorbed." From these passages it appears that their authors consider the seeds or sporules to be formed in the columella, and even of its very substance. Dr. Greville and Mr. Arnott, in their Memoir, object to the opinion that the columella, in the ripe theca, is merely a contraction of the debris of the sporular mass, from the regularity of figure which it often retains, and also from its being sometimes tubular; a fact which, they say, is irreconcileable with the notion of contraction. My observations have convinced me that the sporules are formed from a gummy fluid, which is secreted either by the columella or columellar membrane (most probably by both), and that this secretion becomes cellular by the gradual separation of

the fluid from the solid part; the separation taking place in numberless points throughout the whole mass of secretion. As the little particles of fluid increase in size, the solid material increases in density, until it has assumed the consistence of membrane, which forms an envelope for every separate particle of fluid. Each of these particles, with its investing membrane, then detaches itself from its neighbour and becomes an independent cell or sporule. The following are the facts which have induced me to form this opinion. I find upon puncturing the sporular sac of any Moss in the young state, that a quantity of gummy fluid escapes through the puncture. I find also, that the young sporules always adhere together in masses, if carefully taken out of their natural situation, apparently from being imbedded in an adhesive fluid. The structure of the sporules themselves favours the opinion. In the young state they are remarkably pellucid, and contain a quantity of particles, either in one mass or arranged in *three or four well-defined smaller masses*. These particles I have observed to move with great rapidity. (The species under examination was *Bartramia pomiformis*.) The formation of these particles takes place either during the formation of the cell or very soon afterwards. I have seen the cell in many instances destitute of particles, when, from its extreme transparency, it required a good lens to detect it. The sporule gradually assumes a dark brown colour, and when mature, becomes more or less opake. In some instances it becomes reticulated; in others, granulated on the surface. It is difficult to assign a perfectly satisfactory cause for these appearances. The reticulation, perhaps, depends on the increase in size of the particles within (some of them in the young state being much larger than others); whilst the granulated appearance seems to depend on the hardening and contraction of the membrane. That the sporules are not formed in the columella is clear, as I have frequently dissected off the columellar membrane; and after carefully washing away the sporules, could never detect any in the columella. In the genus *Polytrichum* there is a proof still more satisfactory. The columella, in this genus, has a further separation of its tissue into an axis and a *middle* membrane, between which, in the early state, there is a considerable space, traversed by horizontal fibres. The connexion which these fibres form between the divided surfaces is similar to that which has been already described as

existing between the thecal and columellar membranes. If the sporules were developed in the columella, we should find them occupying this space between the axis and middle membrane: but, on the contrary, they are invariably confined between the middle and columellar membranes.

It will be easy to prove that the sporules are not formed *of* the columella by a breaking up or separation of its tissue: the only foundation for which opinion is, that the columella, in some species, shrinks into so small a space as not easily to be detected; a fact readily accounted for when we consider that, in those instances in which the supposed separation takes place, the cells of the columella are remarkably large, and consequently formed of but little solid material; so that when the fluid (of which in the young state the cells are always full) is dried up, the tissue contracts to the bottom of the theca, and is there easily overlooked. I have examined the thecæ of several of the *Phascums*, in which genus the columella generally shrinks very remarkably; and I have always succeeded in stretching out the collapsed organ to its original dimensions. The columella of *Gymnostomum pyriforme*, in an old theca, occupies but a very small space compared with what it did when young. A section of this may easily be stretched to the full diameter, and then it becomes manifest there has been no dissolution of the tissue. The view here given is supported by the following considerations, which also show the probability that the cellular tissue, at least, of all plants is formed in this manner. We know that the elaborated juices of Dicotyledonous plants descend, between the bark and the wood, in the state of a thick viscid fluid called cambium: and we know that there the alburnum and liber are formed. If a delicate longitudinal section of the end of a growing Hyacinth root be made, we shall find, at the very extremity, a soft, thick, viscid fluid covered by the cuticle. A little nearer the bulb are a number of minute points: still nearer, these points are larger and more transparent: nearer still, they are of a considerable size and transparent, until, gradually, they assume the appearance of cellular tissue. There are no vessels in this part; they being gradually sent downwards from the bulb after the cellular tissue is formed.

Lastly, the sheath of viscid fluid, which, by becoming cellular, connects the seta with the vaginula, may be cited in corroboration. The cellules of

Bovista giganteum have been computed by Dr. Lindley, in his valuable Introduction to Botany, page 7, to increase at the rate of sixty-six millions in a minute. I cannot conceive any mode by which this astonishing rapidity of development can possibly occur, but by the rapid secretion of fluid material, which instantaneously separates at innumerable distinct points into its solid and aqueous constituents.

We have now, I flatter myself, obtained knowledge of the structure of the organs of reproduction sufficient to enter on the subject of the sexes. As the theory of Hedwig is the only one that has obtained any consideration, I shall confine my observations to that. In the Linnean Transactions, vol. x. p. 312, Mr. Brown says, "The account which the celebrated Hedwig has given of the sexes of Mosses seems to be founded on so ample an induction, and is now so generally received, that it must be unnecessary to notice the arguments which mere theoretical botanists have, from time to time, produced against it." Dr. Hooker observes on this subject, in a note to the second part of the *Flora Scotica*, "The more intimately we become acquainted with the reproductive organs of the *Acotyledonous* or *Cryptogamic* plants, the more apparent is it, in my opinion, that there are no sexes, as in the *Phœnogamous* plants, no stamens and no pistillum, nor anything analogous to them; consequently no true *seed*, which can only be produced through their cooperation. The structure of the *seeds* themselves (more properly *sporules*) tends greatly to confirm such an opinion, there being, in reality, no distinction into *cotyledon*, *radicule* or *plumule*, in short, no embryo, any more than there is in the little bulbs seen upon the stalks of the Onion tribe, and upon the *Polygonum viviparum*, &c., which yet equally produce perfect plants. A *sporule* has alike the power of producing from every part of it, either stem or root, as circumstances may require: but it is quite otherwise with the true seed." Dr. Greville and Mr. Arnott in their Memoir remark, that "It is extremely improbable that Acotyledonous plants are furnished with stamens and pistils, and that through their agency the seeds or reproductive sporules are formed. This idea is corroborated by the common phenomenon which takes place in those Cotyledonous plants which rarely bring their seeds to maturity; small bulbs (*gemmæ*), analogous to the sporulæ of the *Cryptogamia*, are produced in the axillæ of the leaves, which, when they fall off, strike root at any part indiscriminately,

thus differing most essentially from true seeds, while the new plant which arises from them is equally perfect. This appears also to have been nearly the opinion that Dillenius entertained respecting the propagation of the *Musci*; and it has been confirmed in later times by the celebrated Richard and others."

In the same Memoir we have the following quotation from Sprengel: "'Though,' says this naturalist, 'I have formerly been a zealous advocate for Hedwig's theory of the fructification of Mosses, it has nevertheless appeared to me an insurmountable objection, that the supposed anthers can again produce buds and strike roots, which is certainly the case with regard to the disks of *Polytrichum commune, Bartramia fontana, Bryum palustre, undulatum, cuspidatum, punctatum,* and with those of *Tortula ruralis.* In *Bryum argenteum* we see the buds containing the supposed anthers constantly drop off, strike root, and produce new plants: this I have observed myself times out of number. Still more in point is the experiment first made by David Meese, of sowing the stellulæ of *Polytrichum commune,* containing merely club-shaped bodies, when he found that plants came up, which, in their turn, produced fruit. Another excellent naturalist, Dr. Roth, has made similar observations with regard to *Hypnum squarrosum* and *Bryum argenteum.*'" "He afterwards adds," say the authors of the Memoir, "'It is more probable, therefore, that these supposed anthers are mere *gemmæ,* produced by the superabundance of the juices, and hence surrounded by succulent filaments.'" The latter quotations contain, as far as I have been able to ascertain, the chief evidence against the theory of Hedwig. Although such arguments establish the improbability of the presence of sexes in Mosses, they by no means amount to a proof of their absence. As for the observations of Sprengel and Meese, they are very defective. Mr. Brown, in a conversation which took place about three years ago on this subject, very justly objected to the conclusions drawn from these experiments. From the statement of Sprengel, it does not appear that the supposed anthers were actually seen to grow: and it seems most probable that the growth took place in the axillæ of the scales, which formed the bud containing the anthers. Every one acquainted with vegetable physiology is aware of the great tendency to development existing in the axillæ of leaves, especially in those which form the scales of a bud. To have

made this experiment satisfactory, the supposed anthers should have been detached completely from the scales of the bud; or the growing bud should have been dissected, and the new parts have been traced distinctly to the anthers. The first experiment I have tried, but only in one instance. It did not corroborate the statement of Meese, although the subject of the experiment was the same species as that which he employed,—*Polytrichum commune*.

The most satisfactory refutation of the theory of Hedwig will be found in the anatomy of the pistillum, where the impregnation of the seeds is supposed by him to take place. It is strange that the structure of this organ should have been so long misunderstood; that the young theca, under the name of germen, should have been supposed to be concealed in the bosom of the pistillum; a supposition of which there is not the shadow of a proof. If we refer to the description in the first part of this paper, we shall find that the cavity of the pistillum is occupied, in the first instance, by a single cell; and that this cell always remains at the base of the seta, where it may be found to the very last, tipping the conical extremity. We also find that before one particle of the theca can be formed, the seta must be developed; a process which, in many instances, occupies two or three months after the destruction of the pistillum. It is scarcely necessary to ask, how it is possible that the sporules can be impregnated before the theca, in which they are developed, is in existence. If sexes are to be found in Mosses, they must be sought in the theca; and accordingly we find that various botanists, probably impressed with this idea, have named in succession all the different parts of this organ as performing the function of the anthers. Some have fixed on the columella; others on the peristome; others on the operculum. It is altogether unnecessary to enter on an examination of the truth of these various hypotheses, as their original proposers have adduced so little in their support, that no one at present considers them worth the slightest attention.

I beg leave to submit to the notice of physiologists the following view of the nature of the sporules. After a series of observations, I am led to believe that the sporules of Mosses, and I may add, of all cellular plants, are analogous to the pollen of the *Vasculares*, slightly modified by circumstances, but agreeing

in every essential particular. In support of an opinion so opposite to any hitherto proposed, I offer the following evidence*.

The analogy of the development of the sporules to that of pollen is very striking even to a superficial observer, and has not escaped the notice of botanists. A section of the anther of the common garden variety of *Primula vulgaris*, taken from a bud when about the size of a small pin's head, exhibits a structure which may be compared to a section of the theca of *Polytrichum*. In the former we find an axis of dense tissue (the connectivum) surrounded by the cuticle. This axis is not central, but placed nearer to the cuticle, on the back of the anther, and may be considered as the columella; whilst the cuticle will represent the theca. A separation of the tissue gradually takes place, in four distinct points, nearly at equal distances from the axis. As the axis is not centrical, these points lie towards the front of the anther. Between each of these points the cuticle is furrowed longitudinally, so that the section has somewhat of a quadrangular figure. The theca of *Polytrichum* merely differs from this in having a complete separation of its tissue all round the axis instead of in four points only. The spaces caused by the separation (not *dissolution*) of the tissue, gradually enlarging, form the cells of the anther, in which the viscid secretion takes place. This secretion is afterwards converted into pollen, in a manner similar to that in which the sporules are formed. When the anther is nearly ripe, a still further separation of the tissue takes place, and the four cells become two. When perfectly mature, these cells

* Since this paper was read, Mr. Brown has called my attention to a memoir by Professor Hugo Mohl (see *Flora*, No. 5, February 1833, p. 65, *et seqq.*), in which the same views are advanced and supported at considerable length.

I may also mention that on the second evening of the reading of this paper Professor Agardh of Lund, who happened to be present, informed me that he had maintained a similar view to the one above as to the nature of the sporules of the *Algæ*, in a work which he had published, but which had not found its way into this country. [The work here alluded to is probably the second volume of the *Lehrbuch der Botanik*, of which a German translation appeared at Greifswald in 1832.]

I am aware that Mons. Palisot de Beauvois endeavoured to prove that the sporules were pollen. He maintained that the sporules impregnated the seed (which he fancied he had discovered), like the pollen of Phænogamous plants;—a view the very opposite to the one proposed in this paper. Mr. Brown has long since (*Linn. Trans.* x. p. 314.) pointed out the error of M. de Beauvois.

dehisce longitudinally at the lateral furrows. In *Buxbaumia* the theca frequently dehisces longitudinally after the manner of some anthers; whilst in *Solanum* the anther dehisces by a pore at the apex, thus approaching the ordinary dehiscence of the theca. The lining of the cells, or *Endothecium* of Purkinje, may be considered analogous to the columellar membrane. In offering this view of the anther, it must not be understood that I dispute the accuracy of those beautiful laws of Morphology which are now so universally acknowledged. All I affirm is, that the tissue of the anther *separates* in a manner similar to that of the theca, without any reference to the *origin* of that tissue.

Similar as is the origin of the pollen and the sporules, their appearance is no less so. In the very young state, it is impossible to distinguish the slightest difference. They are round or triangular, &c., according to the particular species; they are pellucid, and they contain a few moving particles. As they grow older the moving particles increase in size and quantity; and the enveloping membrane becomes more opake. When the pollen has arrived at maturity, the application of water causes the membrane to burst, and the moving particles to be forcibly ejected. I have frequently observed the same fact in sporules of the Mosses and Jungermannias; and Mr. Brown has recorded a similar occurrence in the Lycopodiums. After describing the capsules, he says, in the *Prodromus Floræ Novæ Hollandiæ*, p. 20, "Semina? ovalia, in cumulo alba, seorsim semipellucida, in aquâ fovillam minutissimam explodentia!" It appears by the note of interrogation after "semina," that Mr. Brown, with his usual sagacity, perceived something of their real nature, although the subject did not receive any further attention.

The observations of modern botanists have thrown great light onh te function of the pollen; and from the observations of Amici and Adolphe Brongniart in particular, "It is now known," says Professor Lindley, Introduction to Botany, p. 264, "that a short time after the application of the pollen to the stigma, each grain of the former emits a tube of extreme tenuity, not exceeding the 1500dth or 2000dth of an inch in diameter, which pierces the conducting tissue of the stigma, and finds its way down to the region of the placenta, including within it the active molecules found in the grain: no one has actually seen the tubes pass further than the placenta; but there appears to be

good reason for supposing that the vivifying matter communicated by the pollen tubes to the placenta is by some unknown means transmitted by the latter to the foramen of the ovulum, through which it finally passes into the nucleus, there to become the new embryo*." It is a well established fact that the embryo, or essential part of the seed, is derived from the pollen, and that the membranes which are produced by the pistillum only act as a protection and channel of nutrition to the embryo, until such time as it shall be enabled to provide for itself. Mr. Drummond, in a paper published in the 13th volume of the Linnean Transactions, proved, beyond a doubt, that the sporules of Mosses germinate by emitting "pellucid filaments" from any points in their surface. I have myself examined the germinating sporules of *Funaria hygrometrica*; and I found that the brown coat burst sometimes in two or three places, but most frequently in one only; and there protruded from each fissure a delicate transparent tube containing the moving particles, which had previously occupied the cavity of the sporule. These tubes, or, to speak with more precision, elongated cells, gradually increased in length, and, from exposure to light, became of a green colour. They soon became jointed, from the addition of fresh cells at the extremities. They then began to branch, and after a time produced leaves.

The only difference that I can find between pollen and sporules is, that the coat of the latter is of a more rigid and opake texture. From this difference it is that the sporules rarely burst in a sudden manner upon the application of water; but when they do, the moving particles are discharged loose in the water, precisely in the same manner as are those of the pollen. In both sporules and pollen it is necessary, to the production of the tubes, that the laceration of the coats should take place slowly.

Without reference to the evidence here adduced, we do not overstep the bounds of probability in supposing that in plants of a complicated organization there exists a necessity that the embryo should be protected by a nidus capable of imparting aliment until it shall become sufficiently organized to be capable of reproducing a plant equal in complexity of structure to its parent. Whilst in the *Cellulares* the process of their growth is so little complicated

* Mr. Brown has actually traced the pollen tubes into the foramen of the ovulum in *Orchis Morio*, *Habenaria viridis* and *Ophrys apifera*. See Linnean Transactions, vol. xvi. p. 742.

that the embryo requires no preparation to enable it to perform its functions.

But, taking into full consideration the facts above narrated, we cannot but conclude that in the *Cellulares*, a provision similar to that of the pistillum in *Vasculares*, does not exist,—the former being capable of reproduction by the mere ejection of its pollen or sporules on the soil.

Professor Lindley has drawn an ingenious analogy between the parts of fructification in Mosses, and the flower of *Vasculares*. He argues, that the peristome and calyptra are modified leaves, obeying the received laws of morphology. Not having an opportunity of examining the proofs, which he draws from examples in the cotyledonous plants, I cannot enter on this subject with any chance of either disproving or confirming his opinions. I can, however, bear testimony to the opinion that the calyptra is a modified leaf. Any one who had seen the young leaves of *Tortula ruralis* growing amongst the pistilla would be struck with the similarity of their appearance. If the small portion of lamina at the base of the excurrent nerve were folded inwards, and united at the margin, it would be almost impossible to distinguish the leaf from the calyptra. Dr. Greville, in his beautiful Scottish Cryptogamic Flora, has unintentionally given a good proof of this fact. His figure of the calyptra of *Leskea polyantha* has two nerves at the base, opposite the fissure, precisely similar to those which are found at the base of all the leaves in the plant.

Since this paper was read to the Society, I have been informed by Mr. Brown that Dr. Mohl has recently published some "Observations on the Development and Structure of the Sporæ of Cryptogamous Plants;" a translation of that part which relates to the Mosses he has most kindly furnished me with. Dr. Mohl describes the cavity between the columella and columellar membrane as being occupied, in an early state, by an extremely delicate cellular tissue, the cells of which lie in horizontal rows, and contain small granular masses, the rudiments of the future sporæ. In most Mosses, he states, the sporæ are four in each mother cell, and they are arranged in a tetrahedral union. He fancied that, in some of the cells, he discovered more than four

sporæ, but, from their very small size, he could not obtain a positive conviction of the fact. According to my own observations, these "mother cells" are the true sporæ, and the bodies which he considers the sporæ are the granular contents, arranged in three or four distinct masses, as I have before described. Dr. Mohl also advocates the propriety of considering the internal membrane as belonging rather to the columella than as forming a lining membrane to the theca, which coincides with the view I have offered of its nature.

EXPLANATION OF TAB. XXIII.

Fig. 1. A very young "pistillum" of *Orthotrichum anomalum* before the bursting open of the tubular style at the apex. The solitary cell is seen at the bottom of the canal.

Fig. 2. A "pistillum" more advanced; the base having begun to enlarge, the apex of the style open, and the second cell formed.

Fig. 3. The pair of cells from the last fig. dissected out.

Figg. 4. & 5. Cells dissected out from more advanced "pistilla."

Fig. 6. Another very young "pistillum" of *Orthotrichum Lyellii*, showing more clearly than fig. 1. the tube passing down to the cell.

Fig. 7. Two primary cells of *Tortula ruralis* dissected out, and one of which is burst open to show the moving particles.

Fig. 8. A section of the tubular style of *Orthotrichum affine*.

Fig. 9. The pistillum of *Orthotrichum Lyellii*, a little before the separation of the upper part to form the calyptra. The style is decayed. The longitudinal folds are nearly peculiar to the species.

Fig. 10. A section of the last. The young seta is in the centre, showing a division or arrangement of the tissue into the axis and cortical layer. The wall of the pistillum has separated from the seta and become plicated. That the pistillum does not enlarge at the base by distention (from the growth of the supposed germen within) is evident, as there is a considerable space between the two.

Fig. 2.

Fig 3.

Fig. 5.

Fig. 4.

Fig 6.

Fig. 7.

Fig. 12.

Fig 1

Fig. 14.

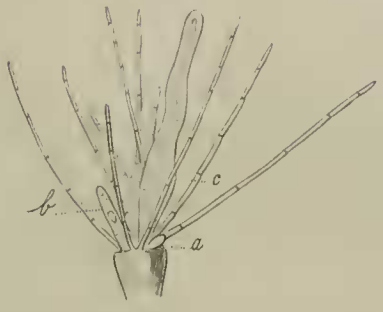

Fig. 9.

Fig. 10.

Fig. 17.

Fig. 19.

Fig. 11.

Fig. 18.

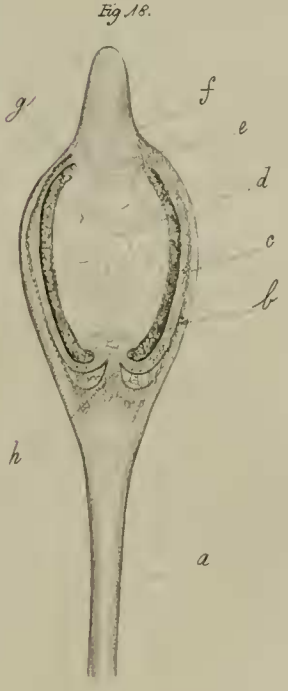

Fig. 16.

Fig. 15.

Fig. 8.

Fig. 13.